Genetic analyses of hunting traits in leashed and non-leashed test systems in Norwegian Elkhound

M. Wetten, T. Aasmundstad & O. Vangen

Taylor & Francis
Taylor & Francis Group

Check for updates

Genetic analyses of hunting traits in leashed and non-leashed test systems in Norwegian Elkhound

M. Wetten[a], T. Aasmundstad[b,c] and O. Vangen[c]

[a]Aninova AS, Hamar, Norway; [b]NORSVIN, Hamar, Norway; [c]Norwegian University of Life Sciences, Norway

ABSTRACT

Norwegian Elkhound Grey is used for both leashed and non-leashed tracking. This study provides influence of fixed effects and estimates of genetic parameters of traits related to both types of tracks. In total, 5393 records from 1991 animals tested in the years 1995–2014 on lashed performance (5 traits), and 5405 records from 2070 animals tested in the years 2005–2014 on non-leashed performance (10 traits) were included in the dataset. The pedigree file contained 8623 animals. Heritabilities were generally low for the non-leashed traits and a bit higher for the leashed traits. Genetic correlations within trait group were very highly positive for the leashed dog traits, but variable among some traits in the non-leashed group. Genetic correlations between performance traits in the two groups were generally negative and unfavourable. Genetic trends were generally positive for the time periods.

Introduction

Norway has seven indigenous dog breeds; of which one is Norwegian Elkhound Grey (NEG). The breed belongs to the FCI group 5 and was in 2015 the top 1 breed in terms of registered dogs in Norway (Norwegian Kennel Club annual statistics; http://web2.nkk.no/no/nyheter/Historisk+topplassering.b7C_wlDSXd.ips). NEG as a breed was created during the early 1800s and appeared for the first time in a Norwegian dog show in 1877. Today, The Norwegian Elk Hound Association has the responsibility for management of hunting trials in the two Elkhound breeds (NEG and Norwegian elkhound black) in Norway. The NEG has sister populations outside Norway, with some genetic influence into the Norwegian gene pool, mainly from the Swedish and the Finnish populations (where the NEG is used for hunting as well). However, all the sister populations were also based on Norwegian dogs only a few generations ago. In Norway, NEG is primarily used for hunting moose, in both leashed and non-leashed tracking. For leashed tracking, the ideal behaviour is to localize and silently lead the handler to the moose. Barking is not allowed, neither is pulling so hard in the leash that loud panting can be heard. For non-leashed hunting, the wanted hunting behaviour is to independently track down and hold moose at bay by barking. Selection is traditionally based on phenotypes from hunting trials. The trials are both social sport gatherings as well as serving the breeding work with phenotypes.

The overall question to be raised is if a selection for the two ways of tracking moose (leashed and non-leashed dogs) is separating the breed into two sub-populations. In order to answer that question, the main objectives of this study were to analyse the data from the two testing systems. Both in order to find correct adjustment factors for fixed effects, to estimate heritabilities and genetic correlations between the traits both within test and between the two tests, to estimate genetic trends for the quality of search for elk in the two test systems and to discuss how the correct breeding goal should be defined in future.

Material and methods

Data

The Norwegian Elk Hound Association provided data on the hunting trials from 1995 to 2014. For the leashed dog trials results, 5394 records (trials) from 1991 dogs were available. The variation in number of trials per leashed dog was between 1 and 10, where 992 dogs had only one start. The same protocol was used for all leashed trials in this period. For the non-leashed dog test, the protocol was extensively changed in 2004/2005. Hence, only the data from 2005 to 2014 was used in the analysis. The available dataset for non-leashed dogs included 5405 records (trials) from 2070 dogs. The variation in number of trials per dog varied between 1 and 6, with 954 dogs having only one start. No dogs have records

in both groups of traits. The pedigree file included 8623 animals going back 10 generations. Imported dogs were included with generally three generations of ancestors available. Average pedigree completeness estimated by EVA software (Berg et al., 2006) was 0.58 with a standard deviation of 0.12. Phantom parents were not created, and there is an expectation that the pedigree completeness is much higher for the younger animals in the pedigree file.

The trials and traits

Trials, both leashed and non-leashed, are held outdoors under conditions as close as possible to true hunting conditions and environments. There are mainly one-day trials in both disciplines. Because of possible interference between dogs, each dog and handler is tested individually and each start is evaluated by one judge. Hence, there is an entanglement between handler, dog and judge. The test terrain within area and judge is drawn randomly. Each recorded trait is evaluated on a score from 1 to 10 where 1 is poor performance and 10 is excellent. If the dog has shown no effort at all, it is graded 0. A dog can enter a trial from 9 months of age. The dog has to be shown at a dog show with prize grade from Excellent to Sufficient to enter the trial. Dogs between 9 and 15 months, however, can start at hunting trial first and attend a show later in order to have the hunting trial registered. This means that there is a slight preselection of dogs based on conformation before the trials. However, this is not expected to influence genetic parameters or genetic trends.

In Figures 1 and 2 are shown the distribution of scores for all traits included in the study. For the leashed traits the distribution of scores is almost normally distributed, however, in the non-leashed traits only NL1 and NL2 shows close to normal distribution. For the other traits, it is obvious that there is a need for a different or new scoring system, as the distributions are far from normal.

The leashed hunting trial includes registration of five separate traits as shown in Table 1. The non-leashed hunting trial includes registration of 10 separate traits as shown in Table 2. The tables include number of records, means and standard deviations for all traits analysed.

Statistical analysis

For the computation of descriptive statistics, we used SAS, General linear models (SAS Institute, Inc, 2007). For the estimation of genetic parameters (heritabilities and genetic correlations) and genetic trends, we used mixed model equations and AI-REML algorithm as the solver. The statistical analyses were performed by using the program DMU (Madsen & Jensen, 2012), using the program package DMUAI. As many dogs had several records, repeatability models were used for all traits. With these models, it is assumed that earlier and later tests have the same genetic background.

The data were analysed according to the following model:

$$Y = Sex + trail\_number + new\_old + age + year\_month + pe + a + e$$

where sex, trail_number and new_old (only for non-leashed traits) are fixed effects, age is a fixed linear regression on age, year_month, pe and a are random effects and e is the random residual.

The significance of fixed effects was evaluated in SAS, and cross-validation was used to evaluate the effect of judge in the model for those years where we had information about judge available. The effect of judge was found to just slightly improve the model, however, it was not included in our analyses as the recent years had no information on judge's identity and would have to be discarded from the analyses. The effect of owner could not be included in the model, as too many owners had only one dog tested and effects of dog and owner would be totally confounded. The fixed effects included were sex with two levels and trial number with four classes (trial numbers 4–6 were treated as one class). Age varied between 1 and 11 years and was included as a linear regression and not a class effect in order to reduce the degrees of freedom used for the model. Random effects in the REML-analyses were permanent environment (pe), additive genetic effects (a) and year_monh (month within year) had 93 levels in leashed dogs and 50 levels in non-leashed dogs. Trials with non-leashed dogs had a minor change in the way of registrations of some of the traits in 2013, therefore a fixed effect of 'new' and 'old' registration method was included. Heritabilities were estimated as additive genetic variance as over genetic and residual variance. Genetic parameters were calculated based on bi-variate models and were relatively consistent across the different bivariate analyses.

Genetic trends were calculated for two of the most important traits, L1 and NL1 (quality of search for elk), based on estimated breeding values for the respective periods in the two groups of traits.

Results

Table 3 shows the significance of fixed effects as well as the amount of phenotypic variance explained by the sum of fixed effects. The fixed effects explained 3%–10% of phenotypic variation in leashed traits and 0.2%–20%
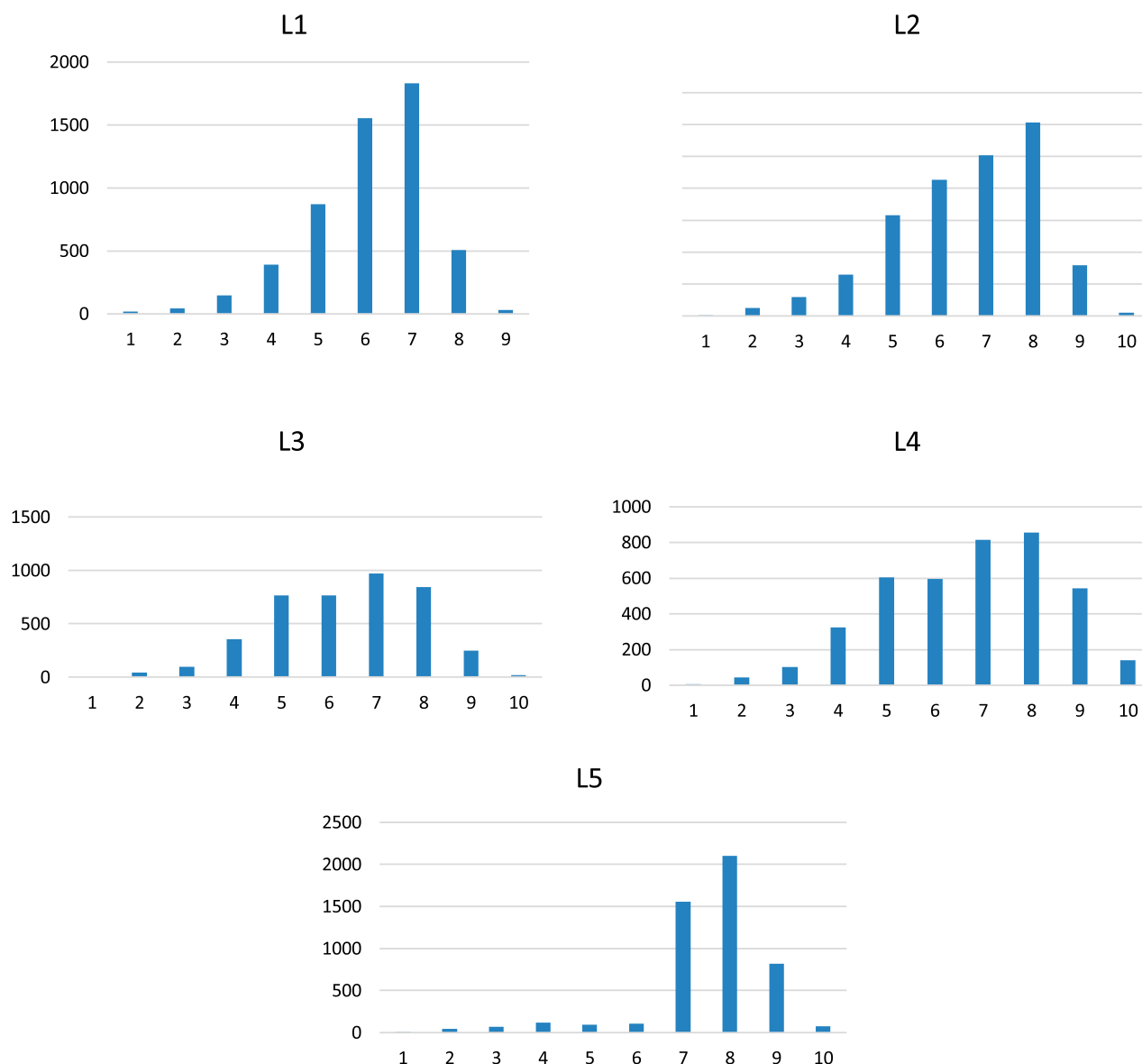
Figure 1. Distribution of scores for traits in leashed dogs (score 10 «the best» in all traits).

in non-leashed traits. The effect of 'new' or 'old' registration system is not presented in the table, but was significant for NL1, NL6, NL8 and NL9. Sex differences were all in favour of females in leashed traits but in favour of males in all significant non-leashed traits. In the leashed traits, traits were improved with age of magnitude of 0.06–0.10 point/year, except for 'Behaviour in front of elk' (L4). In non-leashed traits, traits were improved by age in all significant traits except 'Loudness of barking' (NL7), where the youngest dogs had the highest score.

The heritabilities for the different traits are presented in Table 4. Generally, the heritabilities were lower in the non-leashed traits compared to the leashed traits. Quality of search, ability to find elk, barking and tracking elk show the highest values, while traits including the leader (cooperation and obedience) show the lowest values.

In Table 5 is shown the genetic correlations between traits within the two different tests. The correlations were, between all five the traits in leached group, highly positive. However, in the non-leached group, the results were very variable. Generally, the correlations to the obedience trait NL10 were negative, however, most of them not significant.

In Table 6 is shown the genetic correlations between the traits in the two tests. Most correlations are negative (and thus unfavourable). Some correlations are even quite high and indicate different genetic background for the two groups of traits. However, some of the correlations are not significantly different from zero.

Genetic trends for 'Quality of search for elk' in the two test systems (L1 and NL1) are presented in Figure 1. Both show positive genetic trends. However, when looking at
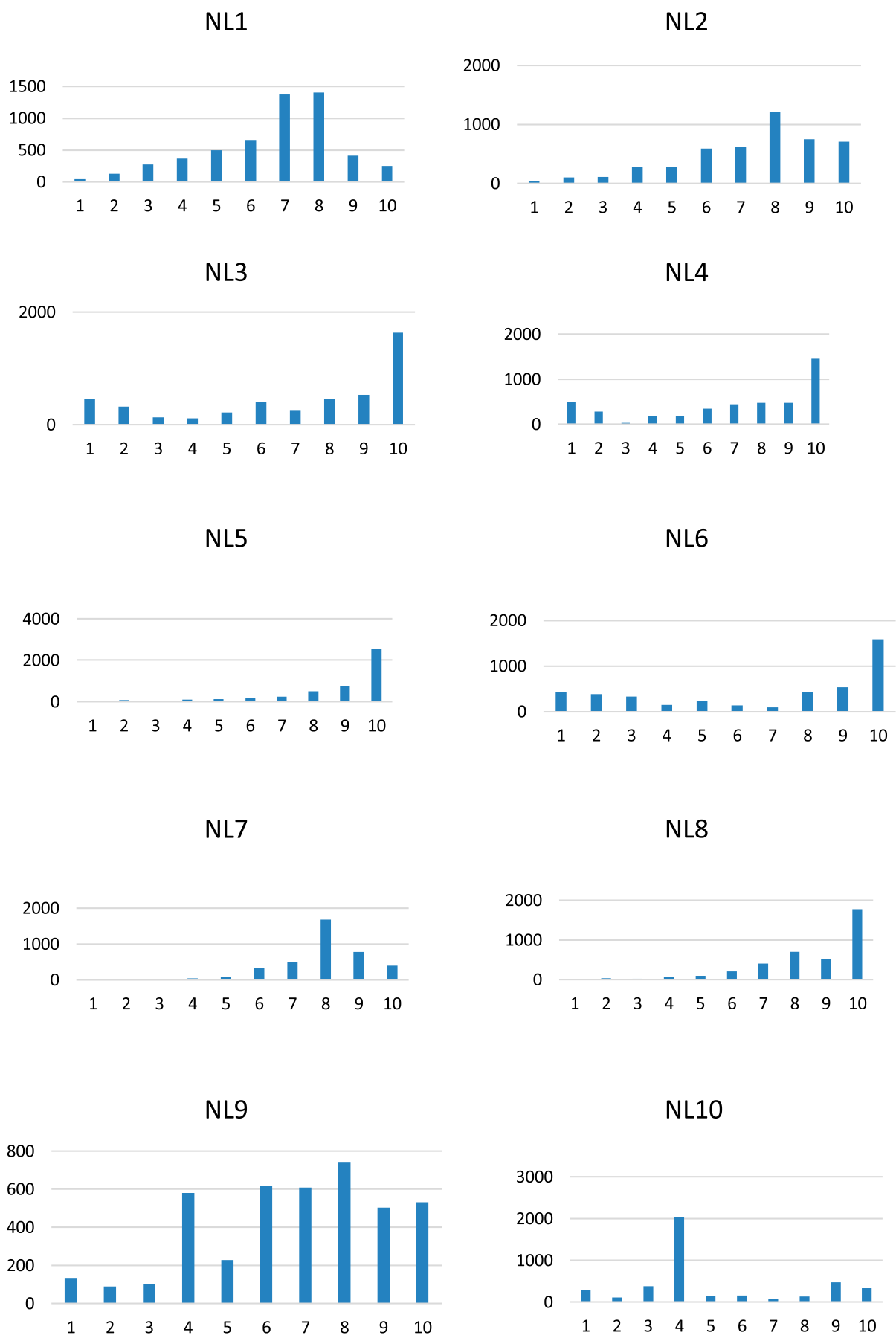
Figure 2. Distribution of scores for traits in non-leashed dogs (score 10 «the best» in all traits).

Table 1. Description of each recorded trait in leashed dogs.

Trait	Number of records	Mean	Standard deviation
L1. Quality of search for elk	5393	7.11	1.29
L2. Ability to find elk	4476	6.62	1.57
L3. Quality of keeping elk at bay	4103	6.37	1.57
L4. Behaviour in front of or when finding elk	4030	6.73	1.79
L5. Tracking elk	5003	7.55	1.32

Table 2. Description of each recorded trait in non-leashed dogs.

Trait	Number of records	Mean	Standard deviation
NL1 Quality for search of elk	5390	6.67	1.93
NL2. Ability to find elk	4655	7.37	2.05
NL3. Ability to keep elk at bay	4506	7.08	3.19
NL4. Quality of keeping elk at bay	4319	7.01	3.16
NL5. How the dog cling to the elk if the elk runs	4564	8.76	1.95
NL6. How the dog conducts itself during baying	4318	6.86	3.38
NL7. Loudness of barking	3834	7.97	1.27
NL8. Use of barking	3795	8.63	1.69
NL9. Cooperation with leader	4112	6.73	2.34
NL10. Obedience to leader	4090	4.99	2.54

Sum points = 100

Table 3. Significance of the fixed effects in the statistical model, including R^2 for the sum of fixed effects.

Trait	Sex	'best'	Season-month	Age	R^2 model fixed effects
L1	0.015	f	<.0001	<.0001	0.07
L2	–	–	<.0001	0.0325	0.10
L3	0.0194	f	<.0001	0.7585	0.05
L4	0.0067	f	0.011	0.0091	0.03
L5	<.0001	f	<.0001	<.0001	0.04
NL1	<.0001	m	0.72	0.0102	0.02
NL2	<.0001	m	0.0004	0.0343	0.04
NL3	<.0001	m	0.0098	0.1472	0.02
NL4	<.0001	m	<.0001	–	0.03
NL5	<.0001	m	<.0001	0.2406	0.02
NL6	<.0001	m	<.0001	–	0.20
NL7	0.5015	–	0.6798	<.0001	0.01
NL8	0.2249	–	<.0001	0.2525	0.02
NL9	0.9012	–	0.0369	0.0152	0.003
NL10	0.5403	–	0.047	0.9406	0.002

L: traits of leashed dogs NL: traits of non-leashed dogs.
'best': the sex with the highest average value. (f = female, m = male).

Table 4. Heritabilities and standard errors (SE) of heritabilities for the different traits.

	Trait	Heritabilities (SE)
L1	Quality of search for elk	0.16 (0.03)
L2	Ability to find elk	0.16 (0.03)
L3	Quality of keeping elk at bay	0.09 (0.02)
L4	Behaviour in front of or when finding elk	0.06 (0.02)
L5	Tracking elk	0.15 (0.03)
NL1	Quality of search for elk	0.08 (0.02)
NL2	Ability to find elk	0.05 (0.02)
NL3	Ability to keep elk at bay	0.05 (0.02)
NL4	Quality of keeping elk at bay	0.06 (0.02)
NL5	How the dog cling to the elk if the elk runs	0.08 (0.02)
NL6	How the dog conducts itself during baying	0.07 (0.02)
NL7	Loudness of barking	0.02 (0.02)
NL8	Use of barking	0.14 (0.03)
NL9	Cooperation with leader	0.01 (0.01)
NL10	Obedience to leader	0.04 (0.02)

L: traits of leashed dogs; NL: Traits of non-leashed dogs.

NEG. Here the trials include a larger part of the population and results from the hunting trials are of the highest importance if to breed champion dogs. However, even in this breed, there is a great need to improve the trials to make them a better tool for breeding better hunting dogs. In NEG, an additional challenge is the two different test systems, leashed dogs and non-leashed dogs are doing very different trials.

The protocol describing the different scores is based on long traditions, however, with changes several times over the years. Based on this study (Figures 1 and 2) there is a need to improve the protocol in order to obtain more normally distributed traits, and some traits should just be recorded as either or traits. Especially in the non-leashed traits NL3-6 and NL8, there seem to be an either or scoring in practice. For these traits, it could be that the different ends of the scale describes different biological backgrounds, however, not possible to explain with the present data.

It has previously been shown, in other hunting breeds, changing the scoring system in order to reach a higher degree of normality has been successful in improving the normality of distributions (Vangen and Klemetsdal, 1988). Our recommendations from the present study, are that the scoring system needs revisions, for some traits to improve the distribution of scores, and for some traits to score them as either or traits.

Generally, the fixed effects recorded do explain only a small amount of the phenotypic variation. As seen from Table 3, there is a tendency that the environmental effects explain more of the variation in the leashed traits. Generally, the leashed dog traits are in practice easier to evaluate, as the dogs are close to handlers/ judges all the time. This is probably the reason for the results in Table 3. The effect of sex shows an interesting pattern with different magnitudes in the two groups of traits (Table 3). The females are doing better scores in

what happened in the leashed dogs from 2005 to 2014, the time period comparable to the time period for non-leashed dogs, there is no genetic improvement in leashed dogs in this period, while in non-leashed dogs the genetic improvement is 0.012 points (or 0.2%) per year.

Discussion

Hunting trials for dogs have several purposes. That is to serve the breeding work, to be a sports arrangement and to create an inspiring environment for those interested in hunting. In many dog breeds, only a small part of the population is taking part in hunting trials, not so in the

Table 5. Genetic correlations with standard errors within the two groups of traits.

Leashed traits	L2	L3	L4	L5					
L1	0.97 (0.03)	1.00 (0.04)	0.80 (0.11)	0.92 (0.05)					
L2		0.98 (0.03)	0.73 (0.11)	0.90 (0.06)					
L3			0.82 (0.08)	0.96 (0.05)					
L4				0.65 (0.15)					
Non-leashed traits *									
	NL2	NL3	NL4	NL5	NL6	NL7	NL8	NL9	NL10
NL1	0.97 (0.05)	0.67 (0.18)	0.57 (0.17)	0.79 (0.13)	0.56 (0.17)	0.38 (0.38)	0.14 (0.21)	ne –	−0.33 (0.29)
NL2		0.77 (0.18)	0.80 (0.16)	ne –	0.87 (0.15)	0.24 (0.40)	0.26 (0.22)	ne –	−0.80 (0.40)
NL3			0.56 (0.18)	ne –	0.37 (0.39)	0.21 (0.20)	ne –	−0.15 (0.34)	ne –
NL4				0.70 (0.13)	ne –	0.30 (0.37)	0.33 (0.18)	ne –	−0.36 (0.33)
NL5					0.62 (0.14)	0.17 (0.34)	0.42 (0.16)	0.88 (0.46)	−0.65 (0.33)
NL6						0.42 (0.37)	0.37 (0.17)	ne –	−0.27 (0.31)
NL7							0.92 (0.34)	ne –	−0.67 (0.44)
NL8								0.97 (0.56)	−0.74 (0.23)
NL9								ne	ne

ne: the analyses did not converge.
*All correlations above 0.40 in absolute value were significant on 5% level.

Table 6. Genetic correlations with standard errors between traits in the two groups of traits, leached (L) and non-leashed (NL).

|	NL1	NL2	NL3	NL4	NL5	NL6	NL7	NL8	NL9	NL10
L1	−0.23 (0.25)	−0.57 (0.26)	−0.46 (0.28)	−0.20 (0.26)	−0.30 (0.24)	−0.69 (0.21)	0.14 (0.50)	−0.07 (0.27)	−0.34 (0.51)	−0.07 (0.39)
L2	−0.11 (0.26)	−0.15 (0.30)	−0.56 (0.27)	−0.44 (0.26)	ne –	−0.59 (0.23)	0.87 (0.58)	0.12 (0.26)	ne -	ne –
L3	−0.19 (0.30)	−0.25 (0.35)	-0.68 (0.29)	−0.61 (0.29)	ne –	−0.63 (0.27)	−0.08 (0.57)	−0.22 (0.31)	ne –	ne –
L4	0.13 (0.34)	−0.05 (0.39)	−0.57 (0.35)	ne –	−0.43 (0.30)	−0.68 (0.31)	−0.27 (0.62)	−0.26 (0.35)	−0.20 (0.71)	0.34 (0.52)
L5	−0.31 (0.36)	−0.54 (0.36)	−0.61 (0.28)	ne –	−0.37 (0.25)	−0.71 (0.22)	−0.34 (0.54)	−0.09 (0.28)	−0.59 (0.50)	0.21 (0.42)

the leashed traits, while the significant sex effects in the non-leashed traits are all in favour of males. Serpell & Hsu (2015) found differences in favour of males in trainability in several dog breeds. However, sex differences in hunting traits are quite different from general trainability. A biological explanation for the present results could be that females are more obedient to the handler and more easily acting together with handler, important in leashed traits. While in non-leashed traits, the males are generally doing better due to the fact that those traits to a higher degree challenge male characteristics (boldness, activity, aggression, etc.). This was shown by Svartberg, (2002) in shepherd breeds. One fixed effect not included in the present study due to incomplete recordings, have been included in many other studies, and shown to have large effects, are the effect of judge (Arvelius & Klemetsdal, 2013, Horn et al., 2017) and/or handler (Lindberg et al., 2004; Lysaker et al., 2014). Our recommendation is to include this information into the data files for future genetic parameter and breeding value

estimations. However, in the present test system, there is difficult to discriminate between effect of judge, handler and the dog effect. Studies of behaviour tests for mentality traits have shown much higher effects of environmental effects such as judge, location, age, and gender (Ruefenacht et.al., 2002).

Generally, there are possibilities to test dogs for general mentality/trainability/obedience, however, already Scott & Fuller, (1975) in their classical book on 'Genetics and the Social Behavior of the dog' state that tests should have different purposes in different breeds and field tests are as well important when breeding of specific traits. The test systems in the present breed are designed for this specific breed, however, divided into two types of trials. One could question whether one joint test could be developed. A test that includes the most important traits from the two test stems.

The higher heritabilities for the leashed traits, shown in Table 4, is also demonstrating the better possibilities for judging the dogs when they are leashed. In non-

Trait L1 "Quality of search for elk"
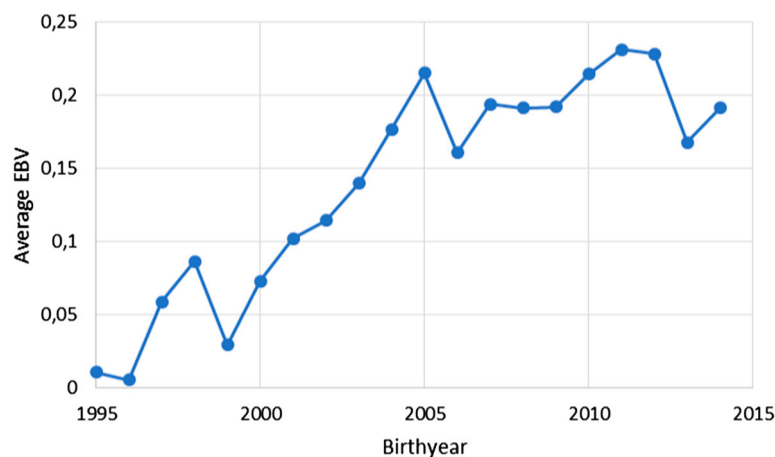
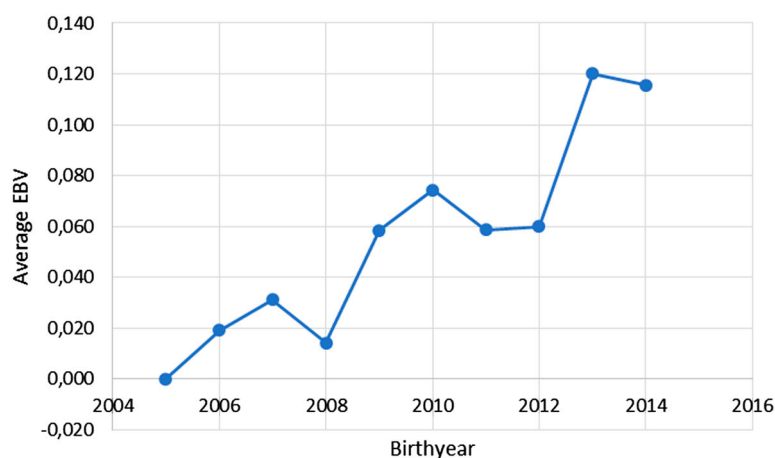**Trait NL1 "Quality of search for elk"**

Figure 3. Genetic trends in the trait Quality of search for elk from both leashed (L1) and non-leashed (NL1) tests.

leashed traits, only NL8, use of barking, shows a heritability above 0.10. Again this is a logical consequence; the judges can hear the sound even if they cannot see the dog. Even if test conditions are not comparable, the heritability estimates are in line with what is found in other comparable breeds or countries (Liinamo et al., 1997; Liinamo, 2009). Some more general ability tests for hunting traits have shown much higher heritabilities, in the area from 8 to 50% (Schmutz & Schmutz, 1998; Arvelius et.al., 2013). As in many other studies, our study shows that traits like cooperation with leader and/or obedience to leader show the lowest heritabilities (Vangen & Klemetsdal, 1988; Liinamo, 2009; Arvelius & Klemetsdal, 2013; Arvelius et al., 2013).

The low heritabilities proof the need for using breeding values as a selection tool in oppose to pure phenotypic selection used in most dog breeds. The question right now is how to use the breeding values in the operating breeding programme. The results of this study show the real big future challenge in terms of not splitting the population in two, as the genetic correlations between the two test systems is not only low, but negative (Table 6). This is even so for the genetic correlation between quality of search for elk in the two test systems (−0.23, however not significant). As is shown in Figure 3, the genetic improvement is present in non-leashed dogs but not in leashed dogs in the comparable period 2005–2014. The genetic correlations between these two test systems could have been influenced by the lack of genetic links. Out of 1076 sires, 210 had offspring tested in both groups. Out of 1725 dams, 227 had offspring tested in both groups.

There are not many estimates of genetic trends for hunting traits in dogs. However, some literature estimates are available especially for hip dysplasia. For example,

Malm et al. (2008) and Wilson et al., (2013) found positive genetic trends for such traits in some breeds.

Future recommendations

Should the most important traits be selected into a joint breeding value? Our recommendations would be that L1, L2, L5 and NL1, NL2, NL5, NL8, the more general and basic traits when hunting moose, could be selected to be included in the joint breeding goal. Not all traits recorded today are of importance also due to the high genetic correlations between traits within test system (Table 5). As the breeding organization does not want the breed to split into two separate genetic sub-groups, it would have been desirable that all dogs should be tested for both leashed and non-leashed traits. When this is not possible because the two types of tests attract different type of dogs and breeders, it is at least important that the breeding values are presented for all important traits in each test system.

Due to the relative small population size (900 pups born annually) and an inbreeding level of 3.7%, with an increase of 0.4% per year for the last 30 years (Wetten & Aasmundstad, 2014), it is important not to split the population in two separate sub-populations. This must be taken into consideration if a joint breeding goal (including test traits) is to be defined. Furthermore, the avoidance of inbreeding should be an important aspect of the breeding programme. A tissue sampling programme is in progress in the breed (at present, >1000 dogs with stored DNA samples) as a part of the research project, in order to create a solid reference population for future studies and for future genome selection studies in dogs.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Arvelius, P. & Klemetsdal, G. (2013). How Swedish breeders can substantially increase the genetic gain for the English setter's hunting traits. *J. Anim. Breed. Genet* 130, 142–153.

Arvelius, P., Malm, S., Svartberg K & Strandberg, E. 2013. Measuring herding behavior in Border Collie – effect of protocol structure on usefulness for selection. *Journal of Veterinary Behavior* 8, 9–18.

Berg P, Nielsen J. & Sørensen M.K. 2006. EVA: realized and predicted optimal genetic contributions. In: Proceedings of the 8th World Congress on Genetics Applied to Livestock Production: 13-18 August 2006, Belo Horizonte; 2006: Communication 27-09.

Horn, S. S., Steinheim, G., Olsen, H.F., Gjerjordet, H.F. & Klemetsdal, G. (2017). Genetic analyses of herding traits in the Border Collie using sheepdog trial data. *J Anim. Breed. Genet* 134, 144–151.

Liinamo, A.-E. (2009). Breeding for improved hunting performance in Norwegian Elkhound and Swedish Jämthund populations in Finland. *Book of Abstracts of the 60the Annual Meeting of the European Association for Animal Production, Book of abstracts No. 15, Barcelona, Spain, 24–27 August 2009*.

Liinamo, A.-E., Karjalainen, L. & Ojala, M. (1997). Estimation of genetic parameters and environmental effects for measures of hunting performance in Finnish Hounds. *Journal of Animal Science* 75, 622–629.

Lindberg, S., Strandberg, E. & Swenson, L. (2004). Genetic analysis of hunting behavior in Swedish Flatcoated Retriever. *Appl. Anim. Behaviour Sci* 88, 289–298.Rhodesian Ridgebacks. *Book*

Lysaker, K., Ådnøy, T. & Vangen, O. (2014). Genetic analysis of mentality traits in of abstracts No. 20 (2014). Copenhagen, Denmark,25-29 August 2014., p. 315. ISSN 1382-6077.

Madsen, P. & Jensen, J.A. (2012). A user's guide to UMU. A package for Analyzing Multivariate Mixed Models, version 6, release 4.6.

Malm, S., Fikse, W.F., Danell, B. & Strandberg, E. (2008). Genetic variation and genetic trends in hip and elbow dysplasia in Swedish Rottweiler and Bernese Mountain Dog. *J. Anim. Breed. Genet*. 125, 403–412.

Ruefenacht, S., Gebhardt-Henrich, S., Miyake, T. & Gaillard, C. (2002). A behavior test on German Shepherd dogs: heritabilities of seven different traits. *Appl. Animal Behavior Sci* 79, 113–132.

SAS Institute Inc. (2007) *SAS OnlineDoc 9.1.3*. (Gary, NC, USA: SAS Instutute).

Schmutz, S. M. & Schmutz, J. K. (1998). Heritability estimates of behaviours associated with hunting in dogs. *Journal of Heredity* 89, 233–237.

Scott, J.P. & Fuller, J.L. (1975). General implications. Part 4 In *Genetics and the Social Behavior of the Dog*. University of Chicago Press. Paperback edition 1975. ISBN 0-226-74338-1, 468pp

Serrpell, J. A. & Hsu, Y.A. (2015). Effects of breed, sex, and neuter status on trainability in dogs. *Anthrozoös* 18, 196–207.

Svartberg. K. 2002. Shyness-boldness predicts performance in working dogs. *Appl. Animal Behavior Sci*. 79, 157–174.

Vangen, O & Klemetsdal, G. (1988). Genetic studies of Finnish and Norwegian test results in two breeds of hunting dogs. *Proceedings of the VI World Conference on Animal Production, Helsinki, Finland*.

Wetten, M. & Aasmundstad, T. (2014). Genetic analyses of hunting traits in Norwegian Elkhounds. *Proceedings 10th World Congress of Genetics Applied to Livestock Production (WCGALP)*. No 793, August 17–22. Accessed 10 January 2018, http://www.wcgalp.org/proceedings.

Wilson, B.J., Nicholas, F.N., John W. James, J.W., Wade, C.M., Raadsma, H. M. & Thomson, P.C. (2013). Genetic correlations among canine hip dysplasia radiographic traits in a cohort of Australian German Shepherd dogs, and implications for the design of a more effective control program. Accessed 6 November 2017, https://www.researchgate.net/publication/258639560_Genetic_Correlations_among_Canine_Hip_Dysplasia_Radiographic_Traits_in_a_Cohort_of_Australian_German_Shepherd_Dogs_and_Implications_for_the_Design_of_a_More_Effective_Genetic_Control_Program.